

Tracts 1966
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(1.)

ELECTRICAL ACTIONS IN NERVES

AND

ALLIED PHYSICAL PHENOMENA.

BY

D. W. SAMWAYS, B.A., D.Sc.

SCHOLAR OF ST JOHN'S COLLEGE, CAMBRIDGE.



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ELECTRICAL ACTIONS IN NERVES AND ALLIED PHYSICAL PHENOMENA.

The chief electrical phenomena observed in nerves group themselves under,

1. Those appearing in damaged, but otherwise unexcited nerves.
2. Those observed in nerves on stimulation.
3. Those arising from the passage through a nerve of a constant current.

It is my intention in this paper to point out some very analogous phenomena of a merely physical nature obtained by the use of a polarisable combination consisting of a metallic wire with a moist envelope.

I. *Electrical phenomena appertaining to damaged but otherwise unexcited nerves.*

In the year 1843 du Bois-Reymond announced that in a nerve cut through transversely the artificial transverse section shows itself electrically negative to any part of the longitudinal surface. The strength of the current observed in a wire connecting the cut end with the longitudinal surface is found—although the resistance introduced is of course greater—to increase with the distance from the end of the point of contact at the surface, until the “equator” or middle point of the surface is reached. Hence the equator behaves as the most

Current in
injured
nerves.

positive, and the transverse section as the most negative, portion of a nerve.

By connecting metallically two points on the longitudinal surface, currents of less intensity ("schwache Längsschnittsströme") pass through the metallic arch from the point nearer to that further from the equator. The strength of such currents increases with the difference of the distance of these points from the nerve equator, and also, like all nerve currents, with the thickness of the nerve; hence two points equally distant from the equator, as also the artificial transverse sections themselves, are found on connecting them to be electrically alike, no current passing.

The term "current of rest" may be employed (after Hermann) to indicate that obtained from an injured resting nerve.

II. *Electrical phenomena observed in nerves on stimulation.*

The same year du Bois-Reymond announced the discovery of a current obtainable from a nerve with an artificial transverse section, he pointed out that it diminished in strength—"negative variation"—if the nerve were at the same time tetanized. The galvanometer needle deflected by the nerve current falls back towards zero, which however it never crosses unless by the mere influence of its own inertia. This diminution is found not to depend on any alteration in the nerve resistance, for not only can no such alteration be observed, but the variation appears also if the rest current be previously compensated; nor does it arise from directly introduced galvanic currents, as electrical stimulation is not essential to its production; it must therefore be due either to an alteration in the strength of the electromotive force producing the current, or to a new and contrary electromotive force. The former view is maintained by du Bois-Reymond, while Hermann, who upholds the latter, applies the term "action current"—as opposed to his "rest current" in unstimulated nerves—to that which results from the new electromotive force developed by the stimulation, and to which the negative variation is supposed due.

Negative
variation
with
tetanus.

Negative variation with single stimulation. With a single stimulation the negative variation in nerves cannot with ordinary apparatus be noticed, and the fact that a contraction can be obtained in a muscle with which a stimulated nerve is in contact at its longitudinal and transverse sections is no proof of its presence, for the contraction in this case is the outcome of a direct electrical action, quite different in nature, belonging to the phenomena of "Electrotonus" (see below). By summing however the effects of several separate stimuli by Bernstein's method with the physiological rheotome—which arranges for connecting a given tract of nerve with the galvanometer between every successive stimulation at whatever rapidity they may be applied—the effect of the inertia of the galvanometer needle is set aside, and the action current, or negative variation, resulting from single stimulation clearly demonstrated.

Measurement of passage rate of negative variation. This method afforded Bernstein a means of measuring the rate at which the changes to which the negative variation is due pass along, i.e. up or down, a nerve. For by closing the galvanometer circuit at varied times after stimulation of the nerve a measured distance away, the electrical condition of the portion of nerve connected with the galvanometer at those times could readily be indicated. It then appeared that the electrical changes took the form of a negative wave whose intensity rose to a maximum and afterwards declined, the wave passing along a frog's nerve at a rate varying between 25 and 32 metres a second; well agreeing therefore with the rate of passage of a nervous impulse obtained by Helmholtz by a method altogether different.

Biphasic action current. Since the negative change passes thus in a wave-like form gradually along a nerve, it would appear that the resulting action current should show two phases when two points on the longitudinal surface of the nerve are connected in circuit with a galvanometer: a first, adterminal in the nerve, occurring when the negative change passes beneath the first electrode connected with the galvanometer, whose deflection should indicate a current towards that same electrode; and a second phase, in which all is reversed, by

the second electrode becoming the more negative as the wave reaches it.

Such a double phase could not be observed in nerves, on account of the rapid passage of the wave along them, till Hermann, adopting the expedient of using several nerves (6) together to strengthen the action by reducing the resistance, and cooling them down considerably to slow it, obtained by this stratagem the two phases; the first adterminal, the second abterminal, in the nerve.

If however one electrode lay on an artificial transverse section, i.e. on a dying portion, the second phase never appeared, thereby indicating that the negative change died out before reaching it, or reaching it was incapable of producing any effect (on a part already so negative). In a perfectly unharmed nerve no phasic action would appear, as the negative change is transmitted along such with undiminished intensity, as well as at a considerable rate.

Trans- verse stimula- tion in- operative.	The above applies only to the case of nerves stimulated longitudinally, for in nerves, as in muscles, transverse stimulation produces no negative variation of the rest current.
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III. *Electrical phenomena arising from the passage through a nerve of a constant current.*

The ad- duced constant current. Galvaic effects.	The honour of initiating researches in this special department of nerve physiology belongs likewise to du Bois-Reymond. He pointed out (also in 1843) that a change was produced in the rest current observed in one portion when he passed a constant current through another portion of the same nerve, the effect depending on and varying with the direction in which the current flowed.
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The effect of the applied constant current shows itself equally in the absence of the rest current, or when the latter is very weak. By suitably connecting the two electrodes of a galvanometer with two points on the nerve beyond the tract sub-

jected to the current, a current is observed in this derived galvanometer circuit like directed to that in the adduced.

The current observed in the galvanometer circuit when a rest current is present, is that due to the latter together with that produced in the extrapolar region by the adduced current, when summed algebraically.

The strength of the derived current varies with that of the adduced, and may be very great, increasing in fact without definite limit (derived currents have been obtained requiring 5 Daniell to compensate them), hence it sometimes considerably exceeds the rest current, and *a fortiori* also the action current. It increases with the length of nerve through which the adduced current flows, the nearness of the latter to, and *cet. par.* the length of, the derived nerve portion.

The position of contact of one electrode of the deriving circuit, whether at the transverse section itself, or on the longitudinal surface, provided it be always at the same distance from the other electrode, is immaterial. In this the effect of the constant current contrasts strikingly with that due to induction, which latter varies considerably in the two cases.

No effects appear if the nerve be ligatured between the adduced and derived districts, but du Bois-Reymond's assertion that in a dead or physiologically discontinuous nerve they are likewise absent requires additional proof. As with an induced, so also with the constant current, no effect is produced if it be applied transversely to a nerve; when applied obliquely the result depends merely upon the value of the longitudinal component.

Du Bois-Reymond styles the constant current the "polarising," and the resultant current the "electrotonic," it will often be better however not to use these terms but speak of the currents severally as the adduced and derived. Neither will it be desirable to rigidly retain after du Bois-Reymond the term "intrapolar tract" for that portion of nerve between the two electrodes of the adduced circuit; thus we may avoid the confusion which results from assuming or denying too much.

When a constant current is passed through a nerve the

Terms
commonly
applied.

irritability of the nerve in the neighbourhood—both extra- and intrapolar—of the electrodes is peculiarly modified; that in the neighbourhood of the cathode becoming more, and in the neighbourhood of the anode less irritable than before the current was applied. The peculiar modified condition into which the nerve is thrown by the constant current is called after du Bois-Reymond the “electrotonic,” the phenomenon being spoken of as “electrotonus.”

Pflüger's experiments show for anelectrotonus that the effects of the application of the constant current, viz. the electrotonic current-actions and irritability-changes, appear simultaneously at different portions along a nerve tract, and are evidently interwoven. Neither has any fixed intensity maximum. “Anelectrotonus”, or the peculiar nerve condition produced in the neighbourhood of the anode of the adduced current, increases and decreases more slowly than “catelectrotonus,” or the altered condition in the neighbourhood of the cathode; it however reaches a higher intensity maximum (see



Fig. 1. After du Bois-Reymond. Time passage and relative intensity of Anelectrotonus and Catelectrotonus. s . Moment of closing. t_1 . Beginning of observation.

Fig. 1). The galvanic appearances are also according to du Bois-Reymond more marked in the neighbourhood of the anode than of the cathode.

Electrotonus is said to require no sensible time for its propagation along a nerve, and though stopped by nerve ligature (for a reason which later remarks will explain) is capable of passing from one nerve to another in longitudinal contact with it, producing in the second nerve like electrotonic actions. If a muscle be in natural con-

Secondary
tetanus.

nection with this second nerve it is thrown into contraction by making or breaking the adduced current, which if made and broken with sufficient rapidity may produce a secondary tetanus in the muscle. This secondary tetanus is easily proved to be the result, not of action-currents as formerly supposed, but of electrotonus; otherwise it should appear with mechanical and chemical stimulation, and require the stimulated nerve to touch the second with points on its longitudinal and transverse surfaces, not appearing, as they do, when the nerves lie merely in longitudinal contact. The presence of this secondary tetanus, as also of electrotonus, may moreover be directly indicated by the galvanic changes observable in the second nerve itself.

As for the rest current, in which a negative variation results on tetanizing the nerve, so has Bernstein shown for an adduced constant current, in which there is a decrease in strength (negative variation) when the nerve to which it is applied is tetanized.

A galvanometer being situated in the circuit of the constant current, and the magnet reflection if necessary brought back into the field of view, on stimulating the nerve beyond the anode a powerful deflection of the needle occurs; beyond the cathode however even strong stimulation produces no alteration in the constant current. This variation in the adduced current on stimulating a nerve is not due to any change in the nerve resistance.

The stimulation of a nerve subjected to a constant current affects not that current merely, but causes also a variation in its dependent current derivable from the extrapolar district. In a nerve with adduced and derived circuits arranged as in the figure, when the stimulating electrodes are applied beyond the

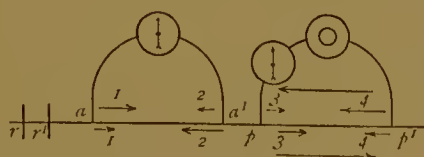


Fig. 2. After Hermann. Phases of the action current in polarised nerves.

derived circuit the action is always of a twofold ("doppelsinnig") character and the resultant currents take the directions indicated by the arrows, the galvanometer in the deriving circuit (*A*) being deflected in a manner indicating first a current opposite, and then similar to that in the adduced circuit. The second phase is always stronger when the derived nerve district is in the anelectrotonic, and weaker when in the catelectrotonic condition.

Many other phenomena have been observed connected with the action of a constant current on a nerve, not the least important being those appearing when the current ceases.

On removing the adduced constant current its effect quickly decreases, and a current may be derived from any portion of nerve beyond the anode whose direction is the opposite to that of the adduced current. If therefore the deriving circuit be closed while the adduced circuit is both closed and opened, a current like and then oppositely directed to the adduced will be observed in it. Fick, who introduced experiments on the after electrotonic currents, believed at first the extrapolar reversal on breaking the adduced current applied also to the extra-cathode district; later however he agreed with Hermann that the eathodic extrapolar after-current was like directed to the adduced: hence, in nerves, both the extrapolar after-currents are adterminal in direction.

As electrotonus is stronger beyond the anode than eathode of the adduced current, so likewise the anelectrotonic extrapolar current is greater than the catelectrotonic; and, by means of an experiment with crossed nerves arranged as in the figure, it may be shown that the after-current in the deriving galvanometer circuit *CBA*, on breaking the current passed through *xBy*, takes the direction indicated by the larger arrow. This is because the reversed after-current in *BA*, beyond the anode of the nerve portion *By* to which a current was applied, is stronger than that in *BC*, which, situated beyond the

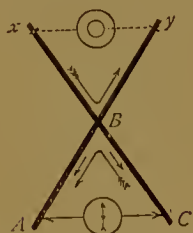


Fig. 3. An- and Catelectrotonic extrapolar after-actions described in the text.

cathode of the same current passed through xB , has its after-current like directed to the latter, and therefore oppositely directed to the after-current in BA .

In the intrapolar region the after-current is, naturally, stronger than in the extrapolar, and is always oppositely directed to the applied current.

It is easily seen from the above that if a series of conductors be arranged as in the figure, by which the after-current from



Fig. 4. From Hermann. Intra- and extrapolar electrotonic after-actions.

various nerve portions may be derived—the adduced circuit being (for convenience in drawing) indicated above, and the derived circuits below, the horizontal line representing the nerve—the currents on breaking the adduced, would, in the derived circuits, pass in directions indicated by the arrows.

Du Bois-Reymond fails to find the presence of extrapolar electrotonic (derived) currents for muscles. Hermann however not only finds such present, but urges that it is impossible since electrotonic actions show themselves in the intrapolar tract and reach a maximum at the poles—i.e. on the border of the extrapolar districts—they should there stop suddenly. Muscles in fact behave similarly to nerves as regards their electrotonic currents, only that in muscles the latter are less marked, and for obvious reasons more difficult to observe.

For the intrapolar tract du Bois-Reymond, in a paper published in 1883, points out that immediately after the passage of a current through muscles, nerves, and electrical organs, the appearance of an oppositely directed current is not universal. If the adduced current were very strong, and its closure very short, the usual inner polarisation may not appear, and a like, instead of an oppositely directed current may be observed; or there may be a double (“doppelsinnig”) action, the galvanometer deflection

Electro-
tonic cur-
rents in
muscles.

Lately
published
secondary
electro-
motor ap-
pearances.

indicating first an opposite, then a like directed after-current. Du Bois-Reymond considers the oppositely directed current as the expression of a true "negative" polarisation, and speaks of the like directed as resulting from what he is pleased to call a "positive" polarisation (see below, p. 26).

THEORIES ON NERVE ELECTRICAL PHENOMENA.

The various phenomena which have now been referred to appear the less valuable and more complicated through lack of knowledge of some definite principles underlying and associating these actions; several theories have been attempted for their explanation, of which the most noteworthy are those of du Bois-Reymond and Hermann, most other theories being more or less modified forms of one or the other of these.

The molecular theory may be stated shortly as follows. The electric current observed on connecting two points on a nerve

The molecular theory of du Bois-Reymond.

is due to the presence in the nerve of peculiar electromotive molecules suspended in an indifferently conducting medium. These molecules ("peripolar") are considered to be made up of two ("bipolar") molecules arranged so that their positive poles lie together in the middle, and their negative poles remote from one another at the ends of the molecular combination. The molecules lie with their longitudinal axes parallel to that of the nerve, and by their sequence form a series of rows or columns in its substance. Thus arranged the action of every molecule except the last in any column is neutralised by that of its neighbours, so that the current obtainable at any time from a nerve with transverse section would be due merely to the combined actions of the free portions (the external dipolar halves) of the terminal molecules of the columns.

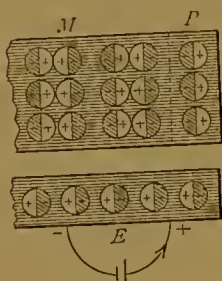


Fig. 5. Du Bois-Reymond's electromotor molecules.

M. dipolar molecules in peripolar arrangement.
P. paraelectronic layer.
E. electrotonic arrangement.

The similar electrical actions observed in muscles du Bois-Reymond explained by the same molecular theory, but soon complicated it to account for the fact that in an uninjured muscle no current appears. It was therefore assumed that towards the ends of an uninjured muscle, a layer (the "parelectronomic") of dipolar molecules did not take the peripolar arrangement, but existed alone, turning their positive poles away from, and their negative poles towards the peripolar molecules, and producing, therefore, an electrical action equal and opposite to, and therefore neutralising, that due to their otherwise free terminal layer. The parelectronomic molecules may sometimes exist several layers deep, and produce the positive, instead of negative, end surface at times observed by du Bois-Reymond on section of a muscle. The development of the parelectronomic condition, and the consequent absence or reversal of a muscle current, is said, though on insufficient grounds, to be favoured by cold.

A parelectronomic layer seems required for nerves as well as muscles, if, as would appear (the experiments of Holmgren on the electrical condition of the optic nerve and its retinal endings being valueless as evidence against it), no pre-existent current obtains in them.

Du Bois-Reymond explains the negative variation of the rest-current on tetanizing a nerve, by supposing the electromotive force of the molecules to decrease, or the molecules themselves to assume a new arrangement by which they become of less external influence.

Electrotonus is explained on the molecular theory, as resulting from the directive action which the adduced current exerts on the electromotor molecules, which, in the intrapolar region, have their dipolar halves so rotated that their positive portions are turned towards the negative electrode and their negative portions towards the positive; their actions are by this arrangement added to one another, and to that of the adduced current. This arrangement spreads out in a less and ever-decreasing degree into the extrapolar district, and explains the electrotonic currents which are there observed. As for the rest-current, the negative variation of the electrotonic currents

on stimulation of a nerve, is assumed due to the strength of the electromotor molecules being thereby decreased.

Du Bois-Reymond's electromolecular hypothesis when first brought out was much simpler than at present, and furnished a suggestive explanation of the then known phenomena; since that time however it has endeavoured to adapt itself to newly discovered facts with very partial and ever-decreasing success. It is ever easy to find a theory to explain a few facts, but the test of its truth is its affording a ready explanation for all facts it bears on, reaching out to predict new, and ever-strengthening itself with the increase in quantity and accuracy of related knowledge.

Thus gauged the theory of du Bois-Reymond is a marked failure, and has come forward to the present day mainly by the impulse which association with his brilliant researches and experiments imparted.

Objections to the molecular theory. Leading objections to the electro-molecular theory as explaining the nerve-currents, besides its artificial assumptions and patchwork nature are,

a (1) When, with time, the current of a nerve with artificial transverse section has considerably decreased, fresh section, as observed by Englemann, may completely restore the original current. It is impossible to explain this by the molecular theory, for if the current decrease were due to diminished strength in the molecules generally throughout the nerve, a fresh section could scarcely restore it. Nor can the decrease be accounted for by loss of function of the terminal molecules, for the same loss through which the molecules fail to furnish the current involves a similar failure in their opposition to the next internal molecules, which being thus set free to act, in proportion as the more terminal molecules lose their power of action, should functionally replace the latter and continue to maintain the current. Fresh section then, by removing unfunctional molecules, should produce no more change in the nerve-current than that due to the mere alteration of the resistance in circuit, which would be comparatively small.

(2) While, theoretically, a fully developed current should appear at the moment of making an artificial transverse section,

Hermann's experiments with the "fall-rheotome" have proved for muscle, that the current is not thus immediately present in full intensity, but increases markedly in amount for a short time after the section is made. A result not only incompatible with the preexistence theory, but with what must be assumed of the nature and conditions of the molecules themselves.

β . Du Bois-Reymond's explanation of the negative variation, as due, either to the electromotive force of the nerve-molecules producing the rest-current decreasing in intensity, or the molecules themselves assuming a new and less advantageous disposition is scarcely more satisfactory, and bears the stamp rather of an effort to reconcile his theory with the facts, than to explain the latter by it. It becomes complicated by having to assume in the case of uninjured muscles that the parelectronic molecules take less part in the change than the peripolar; for were they equally effected, since their actions are opposite they would annul one another, and no negative variation would appear on stimulating an uninjured muscle. The action current in this case therefore must be supposed to originate from the parelectronic layer.

Grünhagen's theory that the negative variation is due to a decrease in the nerve resistance developing an internal shunt for the nerve-current is disproved by the fact, that, if the rest-current be compensated in the usual way, variation in the nerve resistance does not alter the conditions of compensation—for the rest and compensation currents would be changed in equal amounts;—hence the negative variation should not appear on stimulation of a nerve with compensated current, which is contrary to experience.

γ . The failure of the molecular theory is most obvious however where it has to adapt itself to the phenomena of electrotonus. Natural conclusions from this theory are that, if points were taken at equal distances beyond each pole of the adduced current, the irritability of the nerve at corresponding points should be the same, for the extrapolar molecules are like directed in each case and presumably influenced in equal amounts. The propagation of an impulse might however vary according to whether it passed in the current direction or the

reverse; while every part of the intrapolar region, since the directive force of the applied current is uniform throughout, should show the same properties. Moreover, since the electro-motor molecules sum their actions with the adduced current, the apparent resistance decrease of a given portion of living nerve in the intrapolar tract, should, under otherwise similar conditions, be much greater than in the extrapolar, and immensely greater than in a dead nerve.

All these obvious conclusions are however contrary to the observed facts; the condition of nervous irritability in the extrapolar districts are the reverse of one another, one being raised and the other decreased beyond its former value, and in dissimilar amounts, while the transmission of a nervous impulse along a nerve is equally good in both directions. The transition also from the cathodic condition of greater irritability to the anodic of less, takes place in the intrapolar tract, giving rise to an "indifferent point," so that instead of being throughout uniform in character, the intrapolar tract is the seat of three completely different conditions of greater, unchanged, and diminished irritability, passing gradually one into the other. The apparent extrapolar nerve resistance decrease due to the passage of a constant current is found to be greater, instead of less, than that of an equal length of nerve in the intrapolar tract; for while the resistance of the former has appeared to increase 122% by heating, and so killing the nerve, the resistance of the latter has only risen 43% over its original value.

δ. Du Bois-Reymond but last year published a paper on intrapolar after-currents, in which he made a vigorous attempt to defend and advance his expiring molecular theory, his conclusions have however been so completely set aside by Hermann and Hering, that it has but furnished additional evidence of the superfluity, and indeed falsity, of the whole theory (see below, p. 26).

In opposition to the molecular theory Hermann offers quite

another explanation of these varied phenomena.

Hermann's
explanations of
nerve

The parts of a nerve in the neighbourhood of a transverse section would naturally suffer from the injury and commence to die, and where the death of

electrical
pheno-
mena.
The
alterations
theory.

protoplasm occurs, a negative condition as compared to that of more living portions is set up; consequently on connecting by means of a metallic arch, living and unharmed with dying portions of a nerve, an electric current passes through the metal from the first to the second. This, which is advanced in the "alterations theory," explains at once the absence of electrical currents in unharmed nerves and muscles, and their appearance on section or other injury.

The fact, so fatal to the molecular theory of du Bois-Reymond, that a fresh nerve section may completely restore the rest current when it has considerably decreased, indicates merely on the alterations theory that the injury at the section, which is presumably the cause of the current, passes but a short way down the nerve, for instance, to the first node of Ranvier; or, in plants, in which a similar action has been observed by Hermann, to the borders of the injured cells, and there stops. Every new section therefore passes through a fresh portion of nerve unreached by the previous injury, and changes result similar in nature and quantity to those produced by the initial section.

Since then the electromotive force causing the nerve current appears to have its seat at the surface separating dying and living substance, and to depend on changes taking place in the small tract in the neighbourhood of injury, decreasing as these changes decrease and the part dies, reappearing when it is shaved off to expose a fresh and living surface, the current may well be called after Hermann the "demarkation current"; arising, as the alterations theory suggests, from alteration in the injured protoplasm at the nerve ends. (The term "natural nerve current" should be given up, with the term "preexistent"; as any current only appearing after injury cannot be regarded as either natural or preexistent.)

β. In explaining the negative variation of the nerve current on stimulation Hermann urges the analogy between the dying and excitation processes seen in muscle, and says the electrical change might be explained by the assumption that excitation, like dying, alters the protoplasm in such a way that it behaves itself negatively electric towards

the unharmed resting protoplasm. This negative change passes along the nerve from the point stimulated, making the successive points in its course negative to others, and so causing a reverse, adterminal current, the "current of action" which sums itself algebraically with the abterminal, or "current of rest." The negative variation is therefore merely the expression of the action current in the galvanic circuit, as the negative change giving rise to it passes under the first deriving electrode.

γ. The electrotonic currents are regarded by Hermann as branches of the adduced constant current, which spread out into the extrapolar district in consequence of the polarisability of a nerve at the surface of contact of its sheath and contents. To account for their negative variation on stimulation he has suggested the following: "the excitation increases if it passes to stronger anelectrotonic or weaker catelectrotonic nerve places, but decreases if it passes over weaker anelectrotonic or stronger catelectrotonic places."

NERVE POLARISABILITY. OLDER EXPERIMENTS WITH NERVE-MODEL.

It will be necessary in explaining further the electrical properties of nerves, to point out the chief facts and conclusions connected with their polarisability, which exerts a very considerable influence in determining their electrical phenomena.

As far back as 1863 Matteucci pointed out that some of the electrical phenomena of nerves were very similar to those obtainable with an overspun metallic thread, whose sheath was moistened with a conducting liquid.

If two electrodes were applied to the moist wrapping and a current sent through, while two other electrodes connected with a galvanometer were applied at other portions of this pseudo-nerve, a current of like direction to the adduced could always be obtained, which increased or decreased in intensity as the

derived tract was nearer to or further from that through which the current was made to flow.

As this action did not appear if the platinum wire were replaced by one of amalgamated zinc, whose sheath was moistened with saturated zinc sulphate solution, it evidently depended on the wire and its surrounding envelope forming a polarisable combination.

The researches opened by Matteucci were taken up by Hermann in 1871—72, and while made more accurate, were pushed much further. In many experiments he replaced the moist wrapping by liquid contained in a long tube through which the platinum wire was passed, so that the latter was surrounded by a much thicker liquid layer than in Matteucci's experiments. With this arrangement the platinum wire might readily be drawn out and cleaned, the liquid was prevented from evaporation, and either wire or liquid could be easily varied.

A series of side openings were made in the tube referred to, and short open tubes about an inch long sealed into them. The main tube was placed in a horizontal position, with the short tubes vertical; the whole arrangement being filled, even to the mouths of the small tubes, with the same liquid. The current was introduced by suitable electrodes in contact with the liquid in two of the side tubes, and electrodes belonging to the galvanometer, or deriving circuit, were in contact with the liquid in two other tubular orifices.

Using fine platinum wire surrounded with saturated zinc sulphate solution, and employing amalgamated zinc electrodes,—which to prevent their passing beyond the openings of the small tubes into the main had a “bayonet shaped” bend, by which they rested on the tube edges,—Hermann then found;

1. That the derived currents are always like directed to the adduced current, whether derived from the same side of the tube to that of adduction, or the opposite.

2. The derived currents are *cet. par.* proportional to the adduced current.

3. Except from irregular causes, with platinum wire in

saturated zinc sulphate solution or sulphuric acid, they are equal on the side of the anode and cathode.

4. They decrease as the distance between the deriving and adducing electrodes is increased.

5. Other things being equal, the longer the adduced tract the stronger the action, i.e. the influence of the near adducing electrode is all the stronger the further its fellow.

6. By changes in intensity of the adduced current that in a given derived district alters nearly proportionally if the changes are small; by extended intensity changes, the increase becomes relatively less.

7. If the central wire core be absent or distant, or if the continuity of the fluid or core be broken anywhere between the adduced and derived districts, the derived current does not appear. The mutual contact of the two however may be altered or even interrupted—as when a portion of the nucleus is drawn out in a loop from one of the side tubes—the derived current appearing as before.

8. Derived currents do not appear if the combination is unpolarisable, as when amalgamated zinc wire and saturated zinc sulphate solution are employed.

9. They fail also if the adduced current is passed through at right angles to the wire.

10. The derived currents showed themselves simultaneously with the closure of the adducing circuit, the galvanometer being apparently immediately deflected (compare however the results of later experiments given below). If the adduced current continue to flow, the derived current, as indicated by the galvanometer deflection, quickly decreases to a small fraction of its maximum. A quick reversed deflection appears on opening the adduced current, which is all the greater the longer its application, though never quite so large as the deflection observed on closing.

11. The extrapolar districts of both cathode and anode have about the same rate of decrease of their derived currents.

12. If the adduced current and intrapolar wire core be simultaneously interrupted, the galvanometer deflection in the derived circuit is not followed by the reversal which would otherwise occur, the needle merely returning to zero.

13. If the core in the intrapolar tract be broken before the adduced current is made, the effect of the latter is lessened; if after, the extrapolar current decrease appears, but the usual reversal observed on interrupting the applied current is prevented.

14. If one of the adducing electrodes be applied directly to the core end, and the other inserted into the liquid as usual, no reversal appears.

15. The cause of the decrease of the first deflection in the deriving circuit was found not to lie in any decrease in the strength of the adduced current; also the reversal on breaking does not originate in the derived tract, since if the platinum core be broken between the adduced and derived tracts the reversal of the current in the derived circuit never appears; the existence however of two oppositely directed polarised wire districts and a continuous wire core are essential to it.

16. Ramification of the conductor between the adduced and derived tracts, as also the insertion of a metallic bow strengthens the derived currents; they are, on the contrary, diminished by sectional decrease of the liquid in the same district.

Certain variations from the above occur when, as with
 Unipolarisable combination. amalgamated zinc wire in sulphuric acid or sodium chloride solution, or copper wire in sulphuric acid or zinc solution, the combination is polarisable only on one, the anode, side.

On the cathode side the derived currents are very weak, and noticeable only close to the electrode. Unlike with bipolarisable combinations, the derived currents when the combination is unipolarisable rather increase than decrease after their first appearance; the opposite current, which in the former case is developed in the adduced tract, and produces the decrease and reversal, being absent in the latter. Both the extra-

polar after-currents are like, the intrapolar oppositely directed to the adduced current.

These results admit, as Hermann has pointed out, of a ready and obvious explanation. The adduced current instead of passing directly through the badly conducting liquid surrounding the metallic wire in the model, makes use on its way of the better conducting metal core, on entering or leaving which however polarisation is set up which resists its passage, so that to the resistance which the liquid introduces along any line in the current's course, must be added that due to the transition resistance at the surface where the wire and liquid are in contact. If this latter is large in comparison to the passage resistance in the liquid, the current finds an easier course by spreading out further, and though taking a longer journey, enters the core at a position where the polarisation is so much less, that the total opposition to its passage into the core is smaller than by a course more direct.

In this way branches of the adduced current spread out into the extrapolar and intrapolar regions in the manner indi-

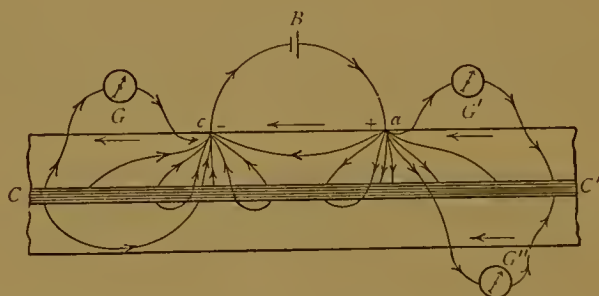


Fig. 6. After Hermann. Current branches spreading out through polarisation.

cated in the figure, the derived currents being merely some of these branches making use on their way between electrode and core of the inserted galvanometer circuit; this explains their appearance only when the combination is polarisable, their dependence on the strength and distance of the adduced current, their behaviour on alteration in thickness of the

sheath or in the length of the adduced and derived tracts, the necessity of the core and sheath being continuous, though not necessarily throughout in mutual contact, the decrease in the derived currents if the liquid section between adduced and derived districts be decreased, the reverse with its increase or the insertion of a metallic arch, their appearance apparently at the moment of adduction, their decrease with its continuance, their reversal on its removal, and their absence with transverse adduction.

The derived currents both indicate the spreading out of the polarisation along the core, and are a measure of the potential difference between the ends of the derived tract. The polarisations at the core increase towards the adducing electrodes, the positive polarisation having its maximum in the section beneath the anode, and the negative in that beneath the cathode. Hence, in the adduced intrapolar district the two polarisations must decrease to an indifferent (transitional) point, in the extrapolar district the polarisation curve approaches the abscissa line asymptotically.

It is easily seen from the figure that the indifferent point must lie in the middle if the polarisations have equal intensity,

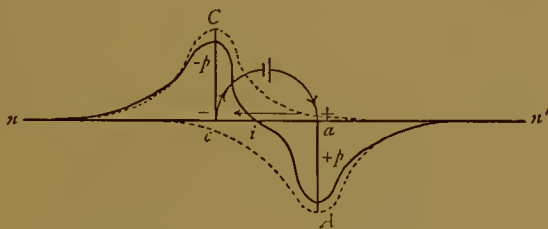


Fig. 7. Superposition of positive and negative polarisation's curve.
From Hermann.

but would be displaced if unequal, and that the polarisation actions interfere with and oppose one another, so that increased distance between the adducing electrodes increases the influence of any given current.

The after oppositely directed current arises as an ordinary secondary action from the two polarisations at the platinum core, and is very weak or absent if the combination be polaris-

able on one side only, or one pole of the adducing circuit be directly connected with the core.

The interest attached to the above mentioned phenomena observed with a purely physical model, is not merely their great similarity to those seen in nerves under like circumstances, but that a nerve itself is in construction and properties comparable to such a model. It consists of a moist envelope (the nerve sheath) and central core (the nerve contents), between which a considerable polarisability exists; thus, the transverse resistance of a living nerve which is from 5—9 times greater than its longitudinal, decreases to only about one-half this amount by the death of the nerve. This decrease is for several reasons attributable to an actual decrease in the specific transverse inner polarisability of the nerve, which would appear to mainly depend on its retaining the living condition. The polarisability of animal parts has been for a long time recognised, as the results of the experiments of Peltier, du Bois-Reymond, Matteucci, and others.

The chief difference between an actual nerve and the pseudo-nerve with metallic core, is in the high conductivity of the core as compared with its liquid sheath, no marked difference in conductivity apparently existing in nerves between contents and sheath. This difference does not involve the appearance of extra-polar currents being due to dissimilar causes in the two cases; for as the nerve-core constitutes a very considerable part of nerve-substance some at least of the adduced current will pass by it, and for such the conditions of entrance and exit will be the same as in the artificial combination, the border polarisation involving the spreading-out of current branches in the nerve-sheath, which form the derived currents, or electrotonic currents of du Bois-Reymond. Professor Weber of Berlin has shown mathematically that the spreading-out of the current branches, when core and sheath have equal conductivities, depends on the value of the transition resistance due to polarisation; they increase with it, reach a maximum, and then again decrease.

The properties of the derived or electrotonic currents in

nerves are immediately explained by this theory, such as their dependence on the length and relative positions of the adduced and derived districts, their absence on any injury, as from a ligature, which may break the continuity of the core substance, and the like.

A nerve also resembles the model in other respects; it is polarisable on both sides, and shows in the adduced tract an indifferent point, displaceable if the polarisation intensity by the cathode and anode vary unequally. Thus with strong currents it passes more towards the cathode, the polarisation at the anode increasing with the strength and time application of the current, while that at the cathode, probably through the anode action being superposed upon it, appears to decrease.

The influence of the form of construction and polarisability of nerves is the key to the action necessary to explain on the alterations theory the appearance of currents when two points on the longitudinal surface of a nerve are metallically connected. An ingenious but less plausible explanation of the passage of the action current wave, based largely on this same polarisability, has also been suggested by Hermann.

The "demarcation currents" arising on section at the surface separating the uninjured and dying substance of the

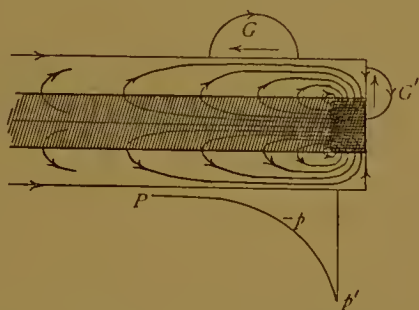


Fig. 8. Spreading-out of demarcation current through transitional polarisation.

nerve, would, through polarisation between the core and sheath, spread out along the nerve in the manner indicated in the figure, the branches returning in the sheath (*schwache Längsschnittsströme*) being obviously those observed when

both galvanometer electrodes are applied at points on the longitudinal nerve surface.

A negative polarisation would be produced along the nerve by the current-branches passing from the nerve core to its sheath, reaching its maximum as the demarcation surface is approached. The latter would explain a given stimulation of a nerve in the neighbourhood of a transverse section having greater influence than elsewhere along its length, and the negative excitation wave when passing towards an artificial transverse nerve section being extinguished before actually reaching it.

The propagation of the action current might, according to Hermann, be due to the negative condition induced in a portion of nerve substance by changes due to stimulation causing currents from the neighbouring more positive nerve portions, passing to the excited negative substance through the sheath, and completing their circuit through the nerve core. Such a passage will produce a negative polarisation in the neighbourhood of the resting, and a positive polarisation in that of the irritated substance. But a positive and negative polarisation are what occur when a current is applied to a nerve, the latter of which is accompanied with an excitatory action upon it; hence the action current following a nerve excitation by negatively polarising the resting substance would excite it, and by positively polarising that already excited would possibly set aside such excitation; in this way therefore might the excitation wave be transmitted along a nerve.

AFTER-CURRENT ACTIONS. LATER OBSERVATIONS.

The paper referred to on page 11, published in 1883 by du Bois-Reymond on secondary electromotor appearances in muscles, nerves, and electrical organs, in which he points out that the intrapolar reversed after-current, observed on breaking the adduced current, is under certain conditions replaced or followed by a current in the same direction as the adduced; and regards

Possible
relation of
polarisa-
tion to the
action
current.

Explana-
tion of
certain
intrapolar
after-
actions.

the latter as resulting from a "positive" polarisation due to the rotation of his electro-motor molecules by the applied current, and as evidence of the presence of such molecules, has had its facts established, but its conclusions overthrown by Hermann.

In his exhaustive paper in Pflüger's Archives published this year, "Ueber sogenannte secundär-electromotorische Erscheinungen an Muskeln und Nerven," Hermann again urges the incapacity of the molecular theory to explain the opposition of cat- and an-electrotonus, and the presence of the intrapolar indifferent point. Having confirmed du Bois-Reymond's statement, that strong currents applied for a very short time favour the like directed intrapolar after-current, Hermann proceeded to show, that a tired condition of nerve was unfavourable to it, while death set it aside; and concluded from his observations, that the like directed after-current depended on the retention of life, and the oppositely directed on the permanence of structure.

Early in his paper Hermann says:

"My first thought on reading du Bois-Reymond's treatise was, that the like directed after-action is nothing else than the action current proceeding from a delaying opening excitation." And later on he proves conclusively, that the like directed after-current is most intimately bound up with the opening excitation, and both in muscles and nerves originates from the anode district. As from Pflüger's experiments the fall of an-electrotonus at the anode will on breaking a strong current produce a strong, somewhat lasting excitation, Hermann's supposition that the like directed phase of the after-current results from nerve excitation is confirmed; and is in full agreement with his theory of stimulated nerve substance causing by its negativity an action current, flowing between more and less positive nerve parts.

Passing on to consider what light his physical model (Kern-leiter-Modell) might throw on the subject of these after-currents, Hermann found, with the combination

Explanation of intrapolar after-currents unsatisfactory on the molecular theory.

Light thrown on

these after-currents by polarisable nerve-model. consisting of a platinum core in saturated zinc sulphate solution,

1. The extrapolar after-action on the anode side, with strong adduced currents, appeared as a quick like directed, preceding the usual oppositely directed current, which became more marked as the strength of the adduced current was increased.

2. With very thin fluid layers, as when moistened overspun wire was used, the after-currents became, in both extrapolar districts, like directed to the adduced.

Hence, since with thin liquid layers the after-currents became like, and with thick oppositely directed, or first like, then oppositely directed to the adduced current, it appeared that by varying the thickness, as by increasing it from thin to thick, of the fluid sheath, the transitional point ("Wendepunct") between these two opposite current actions might be noticed, and its behaviour studied. It was then found, that, as the thickness was increased, this "Wendepunct" first showed itself by the near electrode and gradually passed outwards. An extrapolar after-current derived from beyond this point appeared like, and within it oppositely directed to the adduced current: or deriving from a fixed tract the current would appear like, double (first like, then oppositely directed), or oppositely directed, according to the position of the "wendepunct" in relation to the derived tract, as it varies with varying liquid thicknesses, or current strengths.

Though a reference is necessary, it is not my intention to give even an account of the results worked out and explained in this paper of Hermann's, which would scarcely be understood without a fuller description than is here desirable; the paper itself may be read in Pflüger's *Archives*, Vol. XXXIII. pages 103—168, and having been lately translated in Oxford will probably be shortly published in English.

The extrapolar derived currents observed in the artificial model during closure are still regarded by Hermann as resulting from the spreading-out of current branches due to transitional (polarisation) resistance at the core, while the after-

currents are considered as the consequence of after-equalization actions taking place between the two polarised districts.

In cases where the polarisation occurs at one electrode only, and with thick liquid sheaths, the polarisation, to neutralise itself, requires and causes an after-current, which with positive polarisation (anodic) is directed away from, and with negative (cathodic) towards, the polarised electrode. If the polarisation take place at both electrodes, the neutralising after-currents in the intrapolar and extrapolar districts are oppositely directed to the adduced, the extrapolar turning point ("Wendepunct") being pushed too far out into the extrapolar district for any like-directed current to be observed.

If the wire have but a very thin liquid envelope, as when an overspun wire with its sheath moistened is used, all extrapolar after-currents are like, and intrapolar oppositely directed to the adduced currents.

Muscles and nerves show similar polarisation after-currents to the last-mentioned, with which they more nearly correspond in construction, having a central core with but a thin surrounding sheath.

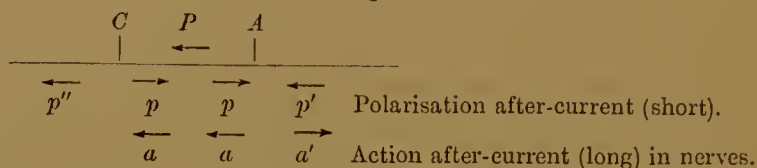
The after-currents may, as stated (page 27), be complicated in muscles and nerves, when a strong adduced current is broken, by the excitation at the anode, which causes an action current, passing outwards from the anode on both sides; that in the intrapolar region being like directed, that in the extrapolar oppositely directed, to the current adduced.

The after-currents actually observed resulting from these two causes, stimulation and polarisation-reversal, will be—since with strong shortly applied currents the polarisation quickly disappears—

1. In the intrapolar tract an opposite, followed by a like-directed current to the adduced.
2. In the anodic extrapolar region they are just the reverse, being first like, then oppositely directed.
3. In the cathodic extrapolar district they are always like-directed.

The direction of these currents Hermann represents in his paper diagrammatically by arrows, thus

Fig. 9.



The series of experiments referred to above on (so-called) secondary electromotor appearances, not only explains therefore du Bois-Reymond's late observations, in defiance of his molecular theory, as the combined result of excitation and ordinary polarisation, but affords a striking illustration of the close analogy between the electrical phenomena observed in a nerve, and those obtainable from a piece of apparatus constructed to resemble it, especially as regards its polarisable properties.

The propagation of the negative changes producing the action current along a nerve at the rate measured by Bernstein of 28 metres a second, has not till now admitted of a very plausible explanation by help of the model with polarisable core. The passage of a wave-like action due to polarisation changes is as yet unknown to electricians, wave-like or oscillatory electrical phenomena having been observed only as the result of induction actions. If polarisation plays a main part in determining demarcation and electrotonic currents, it is to be expected it will play no mean rôle in any satisfactory explanation of action currents, one too less subtle than that suggested by Hermann referred to on page 26.

ON THE PROPAGATION OF GALVANIC ACTIONS IN A WAVE-
LIKE FORM ALONG COMPOUND POLARIZABLE CONDUCTORS.

The experiments which Professor Hermann and I under his direction have lately performed in the physiological laboratory at Zürich, to the number of about 250,

go far to determine what the part taken by polarisation in relation to the action currents probably is. Our results, which were obtained quite separately, and afterwards compared, confirm one another in all points where comparison was possible. They show as their main conclusion, with the utmost certainty, that a galvanic change may be transmitted in a wave-like form along a pseudo-nerve composed of a conducting wire-core and liquid sheath between which marked polarisability exists; which galvanic change is in many respects similar to that which follows the stimulation of a nerve. One great gain of such results is that they tend to throw back into the region of Physics and known sciences the explanation of hazy vital phenomena; at the same time they have a direct physical as well as physiological interest, as casting additional light upon the nature of polarisation itself.

Description of Apparatus and Mode of Experimenting.

All the experiments I performed, numbering nearly 200, were essentially physical, no muscle or nerve being ever used, but their place taken by a piece of apparatus arranged to The nerve-model. roughly resemble them in construction and physical properties. This consisted of a wire, which in almost all experiments was of platinum about the thickness of ordinary sewing thread, which passed completely through a glass tube two metres long, and was fixed by the corks which closed the tube ends. The tube itself had a bore of about 8 mm. and openings along its side to the number of 13, into which smaller tubes, 20 mm. long, were sealed. These tubes, towards one end of the main tube, the adduction end, were set somewhat closely together, being about 4.5 cms. apart, but further along they were separated by about 47 or 48 centimetres; this was desirable, as the actions near the adducing district shaded off much more rapidly than further away. The main tube was fixed horizontally, having the small tubes vertical, and was filled nearly, when necessary quite, to the mouths of these tubes with liquid, usually saturated zinc sulphate solution—hence the wire-core was completely surrounded by liquid, except at such points as it might happen to touch the tube-wall.

The four electrodes belonging to the adducing and deriving circuits were formed of thick zinc wire, having a "bayonet-shaped" bend, and amalgamated.

The two adducing electrodes were usually inserted into two neighbouring side tubes near the end, being thus 4.5 cms. apart, the two deriving were then introduced into two of the remaining tubes, selected according to the purpose of the experiment. The electrodes therefore came into immediate contact with the liquid which surrounded the wire core, but were prevented by the "bayonet-shaped" bend from actually entering the main tube.

To eliminate the action of one electrode in the adducing circuit, instead of being inserted into the liquid it was sometimes connected directly to the end of the platinum core, the other—in this case also of platinum—was inserted as usual into the

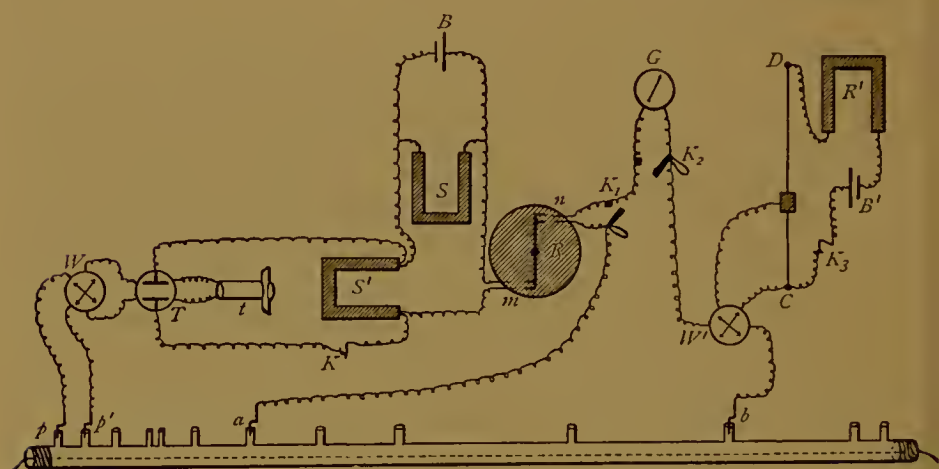


Fig. 10. General arrangement of apparatus.

liquid at one of the side tubes. The whole connections were arranged as shown in the figure, all the parts belonging to the adducing circuit being represented on the left side, and those to the deriving on the right. These were, as far as possible, for convenience' sake arranged on two long tables about a metre apart, between which the observer sat; having the scale and telescope for observing the galvanometer mirror deflections at one end of this space. It was found necessary, however, to have some portions of the apparatus, viz., the rhctome and battery, in another room, for reasons which will be mentioned.

The adducing circuit contained a galvanic cell or cells B, whose poles were often connected with a Siemens' resistance box arranged as a shunt, represented by S in the figure. In some cases the box was placed in the position S' instead of S, beyond both battery and rheotome contacts. One end of the shunt was connected with the main terminal of a wippe T whose cross wires were removed, the other passed to one of the metal banks of the rheotome R, and was there insulated. From the second, near-lying metal bank, a wire passed to the other main terminal of the wippe T mentioned above, having however a mercury key K inserted in its course. Of the four remaining terminals of the key T, two on the one side were connected with a telephone *t*, the two on the other passed to the main terminals of a second wippe key W, in this case retaining its cross wires, and with two of the terminals on the one side of this key the electrodes, which were inserted into the liquid of the nerve-model, were united.

The battery strength in the adduced circuit was varied from a small fraction of a Daniell element, to as much as that of 18 small bichromate cells in series, but in most experiments, a single whole Daniell was used, the shunt resistance box S being then completely removed. In many cases the actual comparative strength of the currents was determined by inserting another circuit, not shown in fig. 10, containing a coil placed close to the galvanometer whose needle it deflected.

The rheotome employed was of the form modified by Hermann from Bernstein's Model, and described by him in Pfluger's Archives, Vol. xxxi. It had two pairs of insulated metal banks, one pair being fixed on the ebonite disc, over which spun a light brass wheel of about equal diameter to the disc,—the periphery of the disc was divided into 100 parts and could itself be rotated by hand, carrying with it, of course, the two attached metal banks.—This pair of banks was inserted in the deriving circuit. The other pair was fixed and placed just beyond the disc. To the brass wheel were attached two pairs of fine wire brushes about 3 centimetres in length, directed downwards, so that when rotated they came in contact with, and thereby united together, the two banks in each pair.

It would be advantageous if these brushes could be fixed on the wheel radially, as when it is driven at high speeds they are often distorted or torn away from their holders by the centrifugal force developed.

The rheotome was placed in another room to that containing the galvanometer, on account of the presence there of the water motor used to drive it; between the motor and the rheotome were inserted multiplying wheels for increasing the speed of rotation. To determine this speed the number of rotations of one of these intermediate wheels in a given time observed on a watch was counted, the ratio between the rotation speed of this wheel and the spinning wheel of the rheotome having been previously determined. The speed could easily be brought to a given rate by altering the supply of water to the motor. The spinning wheel of the rheotome was usually driven at the rate of about 14 complete revolutions a second, and the speed tested as often as necessary during the experiments.

When once properly adjusted the rheotome would work with almost perfect constancy for hours, provided no irregular disturbance took place in the water supply.

The telephone connected with the key *T* was employed to test the thoroughness of the rheotome contacts at *m*, one had merely to apply the telephone to the ear after having thrown it in circuit—and the electrode *pp'* out—by reversing the key *T*.
 Method of determining “contact time.” As it was very desirable to know the actual time during which contacts were made at the rheotome, this was determined by means of a second telephone connected in circuit with a Daniell element, and the two pairs of rheotome contacts. On rotating the ebonite disc, no sound was heard in the telephone until both pairs of contacts were being made simultaneously, and disappeared again, as soon as the closure time of the rheotome contacts for both adduced and derived circuits no longer occurred together. The telephone determination was found to agree exactly with that obtained with a galvanometer.

The time during which the telephone sounded will be spoken of as contact time, it was usually from $1/300$ and $1/400$ second, and is the sum of the closure times of both contact pairs. Of

course the time of closure of any one pair alone could not be determined by connecting the telephone in circuit with that pair only, as it would then always sound. The closure at the adduction contacts m , was probably never more than half the contact time; and in some experiments, in which one brush and bank were replaced by a platinum point and wire after Bernstein's method, the closure had no appreciable duration.

The telephone indicated that during a small portion of the contact time at the beginning, and a longer portion towards the end, contacts were usually very weak, and probably made merely by straggling pieces in the wire brushes: hence the time given as contact time "indicates the maximum time during which the adduced and derived circuits can be regarded as simultaneously closed, even to the smallest degree (the time of closure of the adduced circuit alone, is mainly of interest in our experiments and, as stated, is even less than, probably less than half, the "contact time").

Before commencing an experiment, any current generated at the electrodes in the deriving circuit was balanced. To effect this, the keys K_1, K_2 were closed, and the slide contact moved along the fine platinum wire CD till the galvanometer deflection returned to its original position. The rate of rotation of the rheotome was also observed, and the thoroughness of the rheotome contacts in the adduced circuit tested by the telephone t . Closure of the key K then introduced the adduced current, which was made and broken at the contacts on the rotating rheotome.

RESULTS OF THE EXPERIMENTS.

I. *Bipolar Adduction.*

With the adduced tract about 4.5 centimetres in length, and the first deriving electrode at about the same distance from it, the second deriving electrode being placed much farther away, a series of deflections are obtained on rotating the ebonite disc and thereby varying the time of closure of the derived relatively

to that of the adduced circuit. The values of these deflections as ordinates, with their closure time differences as abscissae can be represented in a curve: four such curves from actual experiments are given in figure I. Ordinates above the base line indicate deflections in the same, below, when in the opposite direction to those produced by like directed currents to the adduced. "Contact time", is marked by the short black horizontal line, while divisions along the base or abscissa line, indicate the time difference in closure of the deriving circuit, by moving the rheotome disc through 1/100th of a complete rotation: from these curves it is evident:—

1. A small deflection caused by currents in the opposite direction to the adduced, gives place, when the two circuits are simultaneously closed, to a strong deflection indicating currents in the same direction, the true first phase of the derived current.

The first phase rises rapidly to a maximum—which occurs generally towards the latter part of the contact time—and then as quickly falls (often however less quickly, depending on the positions of the deriving electrodes), passing over directly into a second or reversed phase. The latter begins after the end of the contact time, rises itself rapidly to a maximum, always much lower than that of the first phase, and then decreases; at first somewhat rapidly, but afterwards very slowly; in almost all cases having not yet disappeared at the end of a complete rheotome rotation. The small deflection observed before the first phase begins is therefore merely the remains of the lasting second phase. With weak adduced currents the second phase often disappears before the end of the rheotome rotation, i.e. in about 1/20 or 1/30 of a second; from its asymptotical mode of disappearance this is probably merely due to the galvanometer having a limit to its sensibility.

2. On removing the nearer or first deriving electrode further from the adducing district, the second electrode remaining fixed, the first phase appears later, it being soon noticed that the maximum may actually occur after the contact time, when the first deriving electrode is somewhat far removed. In some cases, as shown in figures II. and VIII., the whole first phase may appear after

the adduced current has ceased to flow. The curve is at the same time lower and more drawn out, passing over to the second phase much later than when the electrode is near. (See curves referred to).

3. When the position of the first electrode is retained, and that of the second varied, the position of the first phase maximum is not altered (see fig. I.) (a few results suggest it may appear slightly earlier, if the second electrode be approached near to the first), that of the second is however changed, and appears later as the second is moved further out from the first (see fig. II.). This influence of the position of the second electrode practically vanishes after a certain distance, and is never so well marked as the alteration which takes place in the first phase on moving the first electrode. The earlier appearance of the second phase is accompanied with a higher and sharper curve and maximum; but as the second phase increases in height, that of the first decreases (compare the curves *A* fig. IV. and *D* fig. I. with the remaining); this is noteworthy, as the smaller current corresponds with a slightly smaller, instead of greater resistance in the deriving circuit. The first phase probably appears a little later with the distancing of the second electrode.

4. If the distance between the derived and adduced tracts be increased, their lengths remaining constant, the intensity of both phases decreases, and, as shown in fig. III., the first phase appears later and has a later maximum. When the distance was great, it appeared from Professor Hermann's results that the first phase remained as a weak deflection stretching over the whole rheotome rotation, and with no definite maximum.

5. The deflections are often of a double ("doppelsinnig") character; this occurs towards the time of transition from the one phase to the other; the deflection in the direction of the first phase always occurs first, and may persist throughout the whole rheotome rotation. The first deflection increases, the second decreases, in intensity during transition into the first phase; the reverse is the case during transition into the second phase.

The following examples of readings taken during two experiments afford illustrations of these double deflections.

EXAMPLE I.				EXAMPLE II.			
Position of electrodes.				Position of electrodes.			
p	p'	a	b	p	p'	a	b
4.75	56.5	46.7		4.75	9.9	93.5	
←				→			
Battery employed, 2 Dan.				Battery employed, 2 Dan.			
Contact time 96.2 to 1.6.				Contact time 96 to 99.7.			
Rheotome divisions.		Galvanometer deflections.		Rheotome divisions.		Galvanometer deflections.	
Contact time	96		-12	Contact time	95		-20
	97		-11		96	+	0.5-16
	98		-11		97	+	59
	99		-10		98	+	183.5
	0		-12		99	+	315
	1		-11		99.25	+	344
	2		-8		99.5	+	344
	3	+	1-3		0	+	324
	4	+	6		1	+	243
	5	+	16		2	+	192
	6	+	22		3	+	156
	7	+	29		5	+	106
	8	+	31.6		7	+	73.5
	9	+	35.8		10	+	43.5
	10	+	38		14	+	21
	11	+	38		18	+	9
	12	+	40.5		21	+	5
	13	+	38.2		24	+	3.2-11
	14	+	40.5		27	+	3-14.5
	15	+	37		30	+	1.5-17
	16	+	33		33	+	0.5-17.5
	17	+	31		36	+	0.5-21
	18	+	30		39	+	0.3-23
	20	+	23		44	+	0.3-23
	22	+	20		50	+	4.2-24
	25	+	13.5		60	+	0.1-24.2
	28	+	9.5		80	+	0.1-23
	31	+	6		90	+	0.1-24.5
	35	+	2				
	37	+	1.5				
	40	+	0.5-4.5				
	42	+	0.5-5				
	45	+	0.3-7.5				
	50		-10				
	70		-12				

+ indicates first phase deflections, - those of the second phase.

6. That the maximum of the first phase occurred after the adduced current had ceased, when the deriving tract was somewhat far away, was determined without any doubt. That such should be the case is in itself probable, firstly from the tendency of the maximum observed above (p. 36) to appear toward the end of "contact time," and secondly, because a large deflection, often a considerable portion of the maximum, is always observed after the contact time is over if the derived tract be not too near the adduced, even when the maximum appears during "contact time." Becoming accustomed therefore to the appearance of deflections belonging to the first phase, and consequently of currents which they indicated in the deriving circuit, while no current was being simultaneously introduced at the adduced tract, it was almost to be expected that the phase maximum or even the whole phase, should appear, with sufficient distance between the adduced and derived tracts, after the adduced current had ceased. This appearance of the phase maximum or whole phase after contact time was actually observed, and is indicated in the curves figs. II. III. V. VI. VIII.

A platinum point and wire were sometimes employed at one rheotome contact for ensuring sharper and shorter adduction, and more certainly determining the position of the phase maximum.

No effect with induction currents. 7. As was expected, if the ordinary momentarily adduced were replaced by induction currents no effect was observed at all.

Influence of strength of adduced current. 8. The position of the phases was not altered by varying the strength of the adduced current, the influence of such variation was apparently limited to changes in the phase intensities.

To prevent the platinum wire core being markedly altered by deposition of zinc due to electrolysis, the adduced currents were chosen as weak as convenient, and the wire when necessary drawn out and cleaned.

Interrupted wire core. 9. Several experiments were performed with the platinum core broken between the adduced and derived tracts, the two broken ends being drawn a short way out of

one of the side tubular openings, without touching one another, and connected with the two Rheotome banks usually employed for the adducing circuit. The interrupted platinum core was therefore at each rheotome rotation united externally at the same or different times to that of closure of the deriving circuit; the adduced current was in these cases made directly for a few seconds by a mercury key.

Thus arranged the second phase never appears, the first phase lasting throughout the whole rheotome rotation not even falling to zero before a fresh contact is made.

The position of the phase maximum is similarly displaced and altered, with distancing of the deriving tract, to that of previously mentioned cases. (Fig. v. gives curve tracings with interrupted wire core.)

10. If the deriving and adducing tracts be made to coincide by employing the same pair of electrodes for both Deriving and adduced tracts coinciding. circuits, then if the closure of these circuits occur simultaneously, or overlap, a branch of the adducing current passes through the galvanometer circuit (this latter to prevent any chance of injury to the galvanometer should not include the usual galvanometer coil, but a supplementary coil placed at some distance from the needle). Unlike the cases where the derived tract is extrapolar there is absolutely no current between the time of coincidence of the contacts in both circuits, except for an excessively short period varying between $1/1500$ and $1/500$ sec. just after "contact time." Although this short after deflection is due to a reverse current to the adduced, it must obviously pass through the galvanometer in the same direction as the latter, hence the deflection is not reversed, but lengthened out slightly beyond the "contact time." (See fig. IX. which gives four cases.)

II. *Unipolar Adduction.*

11. In this case one electrode (of platinum) only of the Phase appearances, their adducing circuit is inserted into the liquid, and the other directly connected with the end of the platinum

characters and determining conditions. core. Thus arranged the second phase does not appear unless the electrode in the liquid is put in metallic contact with the core between each closure of the adduced current. It is therefore absent if no shunt is present in the adducing circuit, or if the current be broken on the electrode side of the shunt. If a shunt be present and the circuit be broken beyond it, i.e. on the battery side, the case corresponds somewhat to bipolar adduction with single polarizability, and both phases appear (A, fig. VII.).

The curves given in fig. VII. show that metallically joining the electrodes, increases also the strength of the first phase; thus A with a weaker adduced current is higher than B and C; most noteworthy is it that it is higher than C, which having a longer derived tract would *cet. par.* give the greater current (see p. 37).

12. If the positions of the deriving electrodes be varied the phases are varied in a very similar manner to that with ordinary bipolar adduction. Moving the second electrode further away, the first retaining its place, delays the decline of the first phase (compare B and C, fig. VII.), while if the first electrode be moved an experiment of Professor Hermann's (fig. VIII.) shows that at sufficient distance it may cause the whole first phase to be so delayed as not to appear till after the adduced current has ceased; a result quite similar to that given in fig. II. with bipolar adduction.

III. *Results with overspun platinum wire.*

Some of the most instructive results (as being in structure more comparable to nerves) were obtained with platinum wire overspun with cotton. This having been left for hours in saturated zinc sulphate solution, was fixed in two terminal clamps and stretched in a horizontal position, the air in the neighbourhood being kept as moist as possible to diminish evaporation. The wire was painted with zinc sulphate solution when suitable occasion afforded; and thoroughly painted, or preferably resoaked,

before any fresh experiment, which was then performed as quickly and regularly as possible.

The electrodes for both circuits were thick amalgamated zinc hooks hung at measured distances along the wire.

13. When the adducing and deriving districts are very near, the wire, arranged as above, behaves essentially like that in the tube, there being a first phase with maximum at about contact time. The fall however is always much slower and delayed, while the second phase does not appear, unless, as is probably the case, it is indicated by the very marked double deflections which occur during about the last half of the rheotome rotation; these double deflections remain still very conspicuous even when the second electrode is moved some centimetres out.

14. Complete removal of the adduced current, by breaking contact at the key K, is frequently followed by a quick deflection or "kick" in the direction of the second phase deflection, and upon which it is as it were superposed. The features of this "kick" have not been carefully worked out, but it appears to be strongest in places corresponding to the height of the second phase, and least during the height of the first; they are most marked with double deflections.

15. A given alteration in the position of the derived, relatively to the adduced district, produces a greater effect than a similar alteration when the tube arrangement is employed. In fact the wire with thin moist sheath behaves comparably to one surrounded by liquid in a tube whose bore is small, and therefore the liquid resistance considerably increased; a small distancing of the first electrode makes the phase and its maximum much later and lower, as shown in fig. VI.

16. With unipolar adduction the moistened overspun wire behaves much the same as with bipolar, except that there is no trace of the double deflections, so marked in the latter case.

IV. *Other Combinations of Metal and Liquid.*

17. Platinum core with zinc sulphate replaced in the tube by dilute sulphuric acid (5%). Using ordinary "non polarisable" electrodes with zinc clay points, or, what proved better, as introducing less resistance, the usual zinc wire electrodes protected by clay points; the results were essentially the same as with zinc sulphate solution described above.

18. Amalgamated zinc wire in saturated zinc sulphate solution. The combination being unpolarisable, no trace of action occurred.

19. Amalgamated zinc wire in dilute (5%) sulphuric acid. The development of gas bubbles coating the wire made this combination impracticable.

20. Amalgamated zinc wire in half-saturated salt solution. Currents were introduced and derived through clay points. The first phase was quite clearly marked, but only uncertain traces appeared of the second. The action showed itself several times stronger on the anode than cathode side of the adduced current.

21. Platinum wire in fuming nitric acid.

The first phase appeared with certainty, but was very weak. The presence or absence of a second phase could not be decided, the deflection readings, towards and after the end of the first phase, being but fractions of a millimetre. Clay-tipped electrodes were always employed.

22. Copper in zinc sulphate solution.

This was tried by Professor Hermann alone. He says, "The two phases on the anode side of the polarised tract are very beautiful and present as usual; on the cathode side they are significantly weaker, and at times irregular. It is good for the regularity of the results to let the current pass uninterruptedly through the tract for some time before each experiment."

V. *Explanation and significance of the above results.*

The explanation of the first phase appearance has already in past papers been sufficiently put forward and established by Hermann as due to the spreading out of branches of the adduced current into the extrapolar region, on account of the transitional polarisation between the liquid and core, as not to demand any special treatment here. It is enough to observe that our late experiments fully confirm these conclusions, no other explanation can in fact be given of the absence of derived currents only when the combination is unpolarisable, their being more marked the stronger the polarisability, and the manner in which they vary by the adduction being changed from bipolar to unipolar, or the employment of a combination polarisable only on one side.

What has now to be accounted for is, that a momentary current applied to the pseudo-nerve should produce a first phase lasting after the adduced current is removed, and transmitted in a wave-like manner along it, with a maximum ever later with more distant derivation; which may be followed by a second phase much weaker than the first, whose maximum appears later with increased distance of the second deriving electrode.

It would be easy to account for a later appearance of the phase maximum at more distant portions of the model if its appearance only occurred during "contact time", as it might then be attributed to a time-sequence in the development of polarisation along the wire, which latter determines the spreading out of the current branches.

As however, in our experiments the maximum, and even the whole first phase, might be made with distant derivation to appear after the contact time, when the current branches had presumably disappeared, such an explanation by itself is insufficient.

Hermann's late experiments on the appearance of a turning-point ("Wendepunct") in the extrapolar district, depending

for its position on the thickness of the liquid layer around the wire, may presently help towards a solution of the question. The "Wendepunct" occurs at the adducing electrode itself with thin liquid layers, as when Matteucci's moistened overspun wires are used, and far out in the extrapolar district with a thick liquid layer, taking intermediate position with intermediate thickness, and being associated with the behaviour of polarisation equalizing currents. Conclusions from these results applied to the present case would however be premature, if not misleading.

It may be that with polarisation as with induction (for in their reactionary opposition to electrical actions there is a certain rough analogy in their behaviour) a kind of elastic wave-like propagation of electrical changes takes place, appearing only at the make, break, or alteration in the adduced current.

The electromolecular theory could doubtless be made to explain these appearances, were it not fortunately inapplicable to metallic wires and purely physical phenomena.

The second phase which appears with the characters above (pp. 36 & 37) described—I thought, from results obtained among

Relation
between
the second
phase and
changes at
the second
deriving
electrode.

my earlier experiments, could not be due to the passage of some electrical wave-like change under the second electrode comparable to that which Hermann has brought forward to explain the second phase in nerves. This I concluded from results of which Fig. 1. is an example, in which experiments I

was seeking the effect of distancing the second deriving electrode, as I desired to eliminate as much as possible in my future experiments, any influence its nearness might have on the first. I was astonished at the almost perfect similarity between the results obtained, and the apparent indifference of the phases to the position of the second electrode. I found

Apparent
indiffer-
ence to
second
electrode
when
distant.

later this indifference only truly applied when the distance of the second from the first electrode always remained considerable, a change occurring as shown in Fig. IV., when the distances were made much smaller. An

Influence
when near.

indication of this was indeed given in the earlier results illustrated in Fig. I. where the second phase in curve D is much higher than the others; but in that case the correspondence in the time-appearance of the maxima, although the rise of the second phase had increased and somewhat advanced, was misleading, and probably an accident. Had the second electrode been approached to within 4 instead of nearly 19 centimetres, the first phase and its maximum would doubtless have advanced similarly to that of A in Fig. IV.

Finding thus from later experiments that varying the position of the second electrode when near to the first, did materially alter the time-appearance of the second phase maximum, and knowing that the rate of propagation of the wave reckoned when practicable from the time interval between the appearance of the first and second phase maxima, agreed fairly well with that reckoned from the time-interval between the appearance of the maxima of two first phases with two positions of the first electrode, the possibility of the second phase being due to some change propagated as a wave along the model reaching the base of the second electrode seemed after all not so unlikely; further considerations come in, however, which set aside this latter supposition.

1. A first phase may be distinctly marked, with no, or scarcely any, second phase appearing, though the latter may be made to appear by simply altering the conditions in the adduced district in the interval between two adductions. Fig VII. A, shows the appearance of a second phase when, in a tube with unipolar adduction, on breaking the adduced current the electrode in the fluid is left metallically connected with the core, B and C being cases without any such metallic connection.

2. The appearance of the second phase is much more marked and regular with bipolar than unipolar adduction.

3. If the platinum core be interrupted at the rheotome between the adduced and derived tracts (p. 39, IX.), and the adduced currents closed permanently, the second phase is never seen (it would be interesting to try this also with momentarily

adduced currents, the rheotome for this purpose would however require three sets of contacts, the usual two being taken up with the core interruption and closure of the deriving circuit).

It is obvious from the above, that the second phase arises from changes originating neither at the second deriving electrode nor in the intrapolar deriving district, but in the adducing district itself, on breaking the applied current.

The changes in the adducing district producing the second phase, undoubtedly take the form of a current occurring after the current adduction is over, and due to equalizing actions going on between two polarised portions at the wire core. This current passes through the liquid sheath in the opposite direction to that which produced the polarisation. Professor Hermann proved this some years ago for the intra and extra polar oppositely directed currents following the opening of a permanent current.

If the adduced current can produce the first phase, an opposite after-current in the adduced district due to polarisation, being proved, can of course equally account for the second. That such a polarisation after-current produces here the second phase is proved, because the latter fails with a combination, as zinc wire in salt-solution, polarisable on one side only; and, as has been already fully stated, is absent from the combination of platinum wire in saturated zinc sulphate solution or dilute sulphuric acid with unipolar adduction, though always so marked with bipolar. With unipolar adduction, breaking the adduced current leaves the core and electrode externally insulated from one another, and allows no circuit for an after-current; if they are left metallically connected however the polarised electrode and core produce an after-current through the liquid, whose circuit is completed through the metal shunt. With bipolar adduction, breaking the adduced circuit and leaving the electrodes externally insulated, would not prevent a polarisation after-current in the adduced district, both polarisations being at the core, and the second phase consequently always appears.

The most likely explanation of the influence of the position

of the second electrode on the second phase and the time appearance of its maximum (shown in fig. IV.), would seem in its altering the length of the derived tract, and not in its varying its own distance from the adduced. If the first phase last longer with greater length of derived tract,—a very probable supposition, —then must the second phase, which has to wait till the first is over, appear later. This supposition very well explains the later appearance of the second phase with more distant second electrode. The diminished height of the first phase and increased height of the second, observed with the near position of the second deriving electrode (see figs. I. and IV.), confirm this hypothesis. The decrease in the first phase arises from the potential difference at the base of the deriving electrodes being less than when the deriving span is longer. The increased height of the second with shorter span, obviously arises from the second electrode being brought from weaker to stronger polarised parts of one extrapolar region, and so making it possible for the stronger after-current branches, which are passing to the oppositely polarised district, to make use on their way of the deriving galvanometer circuit, instead of flowing merely beneath the foot of the nearer deriving electrode.

As moreover distancing the second electrode when no second phase is present increases the duration of the first, the action of the second electrode cannot be regarded as wrapped up wholly with the appearance of the second phase, and the time fixing of its maximum; its influence is rather that, as stated, arising from the alteration in length of the derived tract, which variation in its position produces.

The production of the second phase is without doubt then due to the polarisation produced, and by the incoming currents maintained, on the metallic core, neutralising itself, in part at least, by after-currents reversed in direction to the adduced; the reversed currents being merely branches of the polarisation currents, as the direct were of the polarising.

This explains the duration of the second phase and its form of decrease. It explains also the double deflections often seen,

lasting sometimes through a considerable part of the rheotome rotation, when the first deflection as the first phase declines is followed by an opposite (example, see page 38) increasing as the first decreases. The core being practically permanently polarised (never being able to more than partially neutralise its polarisation between each current adduction) produces a reversed current whenever opportunity affords, so that there appears a complete second phase if the first phase be over, and double deflections (like and oppositely directed) when the first phase currents are weak. These double deflections are most marked, and apparently always present, when a platinum wire after Matteucci's model, with moist wrapping is used. In this case the simultaneous slow decrease of the first phase, and the permanence of polarisation at the core, arising from the increased resistance of the sheath to the passage of the polarisation neutralizing currents, present the conditions most favourable to the production of these double actions.

It results from what has been said that the second phase is but the expression of a more or less permanent polarisation at the core, the first phase being merely superposed upon the second, and overcoming it by its greater intensity.

The behaviour of other combinations than platinum wire in zinc sulphate solution or dilute sulphuric acid, may now be easily explained.

The absence of transitional polarisation with amalgamated zinc wire in saturated zinc sulphate solution accounts for the absence of extrapolar currents, as without polarisation there is no cause for the spreading-out of branches of the adduced, or the generation of reversed polarisation currents. The small polarisation produced with platinum wire in fuming nitric acid explains the very small deflection seen, while to the lack of polarisation reversal is due the apparent absence of the second phase.

Copper wire in zinc sulphate solution shows both phases when deriving on the anode side, the first only with derivation on the cathode side. Presumably the reversal in the first case is due to a small polarisation at the cathode, as well as the anode,

though theoretically the anode should alone be polarised. Amalgamated zinc wire in dilute salt solution shows only the one phase, and this much stronger in the anodic extrapolar district than the cathodic: this is due to the combination being polarisable only on the one side. If a trace of the second phase occurs, as one or two experiments seemed to indicate, it may be due as in the case last mentioned, to the cathodic district being not entirely free from polarisation.

Considerable interest attaches to the rate at which the wave is propagated along the polarisable conductor. This is best determined by noting how much later the first phase maximum appears, when with the second deriving electrode placed permanently somewhat far away, the first is moved from a position nearer to one further from the adduced tract; if then the distance through which the first electrode has been moved, be divided by the time-difference in appearance of the maxima, the rate is of course obtained. This was not found to be constant in our experiments, but usually varied between 20 and 65 metres a second.

With Matteucci's overspun wire moistened with saturated zinc sulphate solution, I could (on account of the alteration in the moist envelope, through evaporation during the experiment) only determine the position of the maximum satisfactorily by a method analogous to that for determining the zero or rest position with an oscillating balance, where, with decreasing deflections, the mean of two alternate readings of the pointer on the one side equals the true deflection at the time corresponding to that when the intermediate deflection on the other side was taken. Similarly, comparing the deflection with the rheotome disc in one position with that when the disc was slightly rotated, the smaller deflection did not necessarily mean, that the phase maximum corresponded less with the then rheotome position: it might be due—if the smaller deflection were that second observed—merely to the drying by evaporation in the moist sheath. By turning back the rheotome disc to its first position and taking another reading—always allowing about equal time to elapse between each observation—it will be found that the value of this reading will be less than that taken

before with the same rheotome position. But the mean of these two readings may be compared with that intermediately taken with the rheotome in a different position, as error resulting from evaporation at the sheath will be thereby practically eliminated.

Working in this way I fixed two phase maxima for two altered positions of the first deriving electrode, when the rate of transmission of the first wave came out to my astonishment 28·3 metres a second. This remarkable coincidence with the rate of transmission of the negative wave producing the action current in nerves may be an accident, but at all events adds its testimony to that of experiments obtained with the tube to the rate of propagation of the wave in the nerve model being comparable to that along a stimulated nerve.

The rate of transmission of the wave appears from all experiments to be independent of the strength of the current adduced, but is probably somewhat less in moistened overspun wires than in those with thicker fluid sheaths.

It will be manifest from the above that we have found a striking resemblance in the wave-like electrical effects obtainable with a wire core and liquid sheath polarisable at their border surface, and the transmissions of the "action current" along a nerve and muscle after stimulation. Bernstein, as stated (p. 5), has shown that the negative variation (the expression of Hermann's action current) passes as a wave along a nerve; being absent at a part distant from the exciting electrodes at the moment of excitation, but reaching it after a short time, depending on the distance, increasing in strength quickly to a maximum, and then more slowly falling; the wave being transmitted at a rate which in frogs' nerves varies between 25 and 32 metres a second. This wave, as Hermann has observed under certain conditions in nerves, may show two phases.

We find likewise for our physical model, with adduction of momentary currents, an electrical wave, wrapped up in some way with polarisation, which can be picked out at different positions along the model, reaching the more distant later than the nearer, and it may be, after the adduced current has com-

pletely ceased. Its rate, as measured from the time difference in appearance of its maximum at different distances, varies between 20 and 65 metres a second with the tube arrangement, and is about 28 metres a second, apparently, when the moistened overspun wire is employed. A second oppositely directed phase usually appears after the first is over.

The analogy is increased not merely by the resemblance in construction of the nerve and model, each containing a central core and surrounding envelope, but by the fact that the nerve, like the model, is highly polarisable at the border-surface between core and sheath. In fact some researches of Professor Hermann's, shortly to be published, show that a nerve possesses an exceedingly high polarisation constant, of an altogether higher order than that between liquids, and comparable rather with that between the more polarisable combinations of liquids and solids.

One marked difference between the two cases is, that along a fresh and uninjured nerve the action current wave passes without decrease in its intensity, while along the nerve-model the wave is constantly weaker at greater distances from the adduced district. As, however, my time abroad was altogether too limited for as thorough an investigation of the phenomena under varied conditions as the subject demands, it is impossible to explain, as it is equally undesirable to urge too strenuously, all the points of difference between the two sets of cases, which, moreover, further experiments may set aside.

These differences, in face of the many striking analogies, need not at present afford any special objection to seeking the explanation of the negative variation of the rest current in nerves, in the transmission of some electrical change along them, determined mainly by their polarisability and form of construction. I intend at the first opportunity to continue my experiments with a view especially to that most valuable of all scientific work, the obtaining of quantitative determinations; till this is done more fully, these researches cannot be regarded as complete.

CONCLUDING REMARKS.

It will be seen from what has been said in this paper, how rich and suggestive are the results obtained since Matteucci's time, by carrying on investigations similar in character to those first introduced by him.

Not only are du Bois-Reymond's electrotonic currents clearly explained as resulting from the spreading-out of branches of the main current, as the result of polarisation—for they can be shown on a polarisable model constructed to imitate a nerve as well as on nerves themselves—but Hermann has likewise (as described above, p. 29) imitated, at least partially, on such a model his intrapolar after-currents, i.e. the currents which may be obtained in the intrapolar district, and treated of by du Bois-Reymond as secondary electromotor appearances. Hermann also, after discovering extrapolar after-currents as well in both muscles and nerves, has proceeded to show that they too may be copied in a similar way, and explained as due to the after-equalization of the polarized parts, coupled, in the case of strong currents shortly applied, with the lasting effect of excitation.

The spreading-out of the "demarcation current" (rest current), and the appearance of currents (*schwache Längsschnittsströme*) with derivation from two points on the longitudinal surface of a nerve or muscle, are also simply and beautifully explained, as consequent on transitional polarization.

Likewise also the wave-like propagation of the action current, which appeared least likely to find an analogy in phenomena of a merely physical origin—for the propagation of a galvanic change in a wave-like form determined by polarisation was unknown in Electricity—has been shown by the researches Professor Hermann and I have lately made, to have a striking similarity in character and rate of transmission with such electrical actions, now for the first time observed, which are propagated as a wave along a polarisable combination of metal and liquid, consequent on the adduction and removal of a momentarily applied current.

It is evident therefore from these facts, coupled with the high polarisation constant found for nerves, that the main electrical phenomena of nerves (and from their similarity also of muscles) are largely determined by their form of construction, and merely passive physical properties; and no small advance may be made in discovering the means of obtaining accurate and practical solutions of vital phenomena, if future researches point still to Physics for the key to other of these hidden facts of Physiology.

In conclusion, I must express my great and lasting indebtedness to Professor Hermann, no less for the stimulus and encouragement of his kindness than for his suggestive and invaluable help.

EXPLANATION OF THE CURVE PLATE.

Divisions along the black horizontal or abscissa line indicate times taken by the spinning wheel of the rheotome to pass from one of its scale marks to the next, the value of these times is given for each case. The thick black horizontal line indicates the "contact time." The galvanometer scale deflections are expressed as ordinates, the points being the deflections actually observed, and the curves formed by joining them. Deflections due to currents like directed to the adduced are indicated as ordinates above, those oppositely directed below, the base line.

Double ("doppelsinnig") deflections are indicated by vertical lines from the curve, but are not always drawn.

An outline scheme accompanies each set of curves, p, p' standing for the adducing, and a, b the deriving electrodes, the numbers lying between, express the distances in centimetres between the electrodes in each experiment. The separate curves are dealt with fully in the text.

All the curves are taken from actual experiments.

